

Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia).

1. Laboratory methods and a review of *Palaemon (Paleander) elegans* Rathke 1837

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Synopsis

Nine larval and the first post-larval stages of *Palaemon (Paleander) elegans* are described from specimens reared in the laboratory. The results are compared with data of previous authors concerning larvae and post-larvae from different parts of the known geographical range of the species, both for larvae reared in the laboratory and material from plankton samples. The number of larval moults (6-9) is influenced by environmental conditions, especially temperature.

Introduction

Larval stages of British decapods are poorly known and in 1974 a programme was started in the British Museum (Natural History) to study larval taxonomy of British prawns and shrimps (sub-order Natantia). The overall strategy of this series of papers is:

1. To provide detailed descriptions of all larval stages both for the purposes of identification and as the basis for a future systematic study involving the use of numerical methods.
2. To study morphogenesis and reproductive patterns, especially the variability of structure and differing numbers of larval stages.
3. To review previous work and correlate this with the results of the present research programme.

It is appropriate in such a study to bear in mind the caveat of Gurney (1924): 'A certain amount of caution is necessary in accepting a series of stages as determined under artificial conditions as normal. I have found myself in the case of *Palaemonetes varians* that abnormal intermediate stages may be obtained in captivity . . .'

Materials and methods

Circulation system for adult-holding bank

Ovigerous *Palaemon (Paleander) elegans* were collected by handnetting from mid- and low-shore rock pools at Rottingdean, Sussex, England (grid reference: TQ 373019). The species was easy to obtain and served both to test the rearing equipment and to complete the description of larval stages from British waters ably begun by Gurney (1924), but unfinished. Adult prawns were kept in 'Plymouth' sea water (supplied by the Plymouth Marine Laboratory) in a closed circulation system housed in a controlled temperature room at 15 ± 0.5 °C. A light régime from 0600 to 1730 h was provided by two 1.46 m daylight fluorescent tubes situated 1.5 m from the holding tanks. The animals, which were fed every 2-3 days with dried small crustaceans ('Hykro Shrimp Snack'), survived for several months in the holding bank.

The circulation system (Fig. 1) maintained a supply of clean, filtered sea water. Water from the header tank (Fig. 1a) ($45 \times 45 \times 45$ cm), holding approximately 70 l, gravity feeds through an isolation valve (Fig. 1b) to a distribution pipe (Fig. 1c) which gives equal water pressure to six clear plastic containers with lids (Fig. 1d) ($9 \times 15 \times 27$ cm) in which berried females are held.



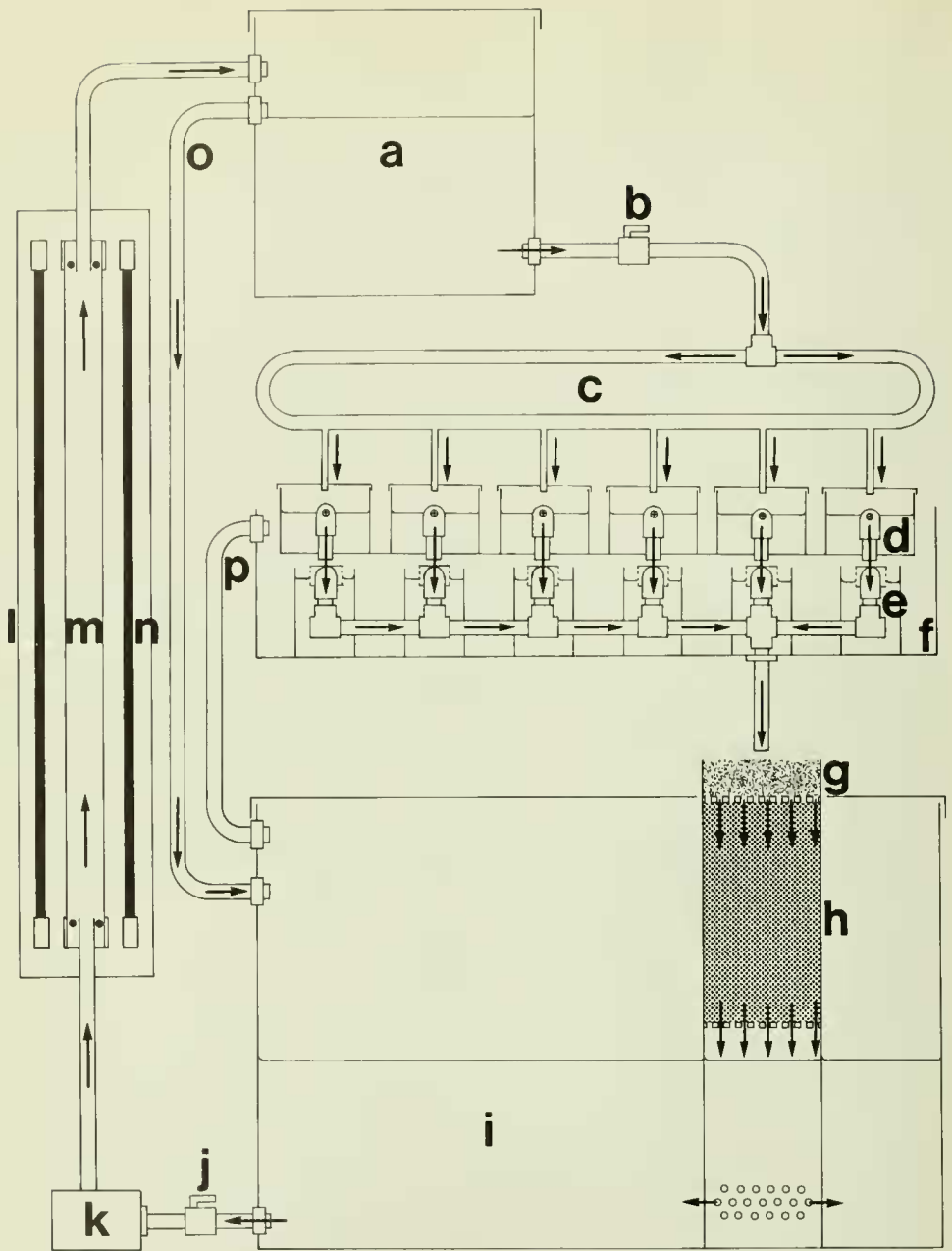


Fig. 1 Sea water circulation system: (a) header tank; (b) valve; (c) ring main; (d) adult-holding containers; (e) larval trap; (f) shallow tray; (g) synthetic fibre filter; (h) biological filter; (i) reservoir; (j) valve; (k) pump; (l) outer alloy case of ultra-violet filter; (m) quartz tubing; (n) ultra-violet tubes; (o, p) overflow pipes. Arrows show direction of water flow.

These containers are supplied with sea water at a rate of 30–35 l/h (providing a complete water change every 6 minutes). The outlet from these containers is guarded with a coarse plastic mesh to prevent the escape of the adult. The larvae, which hatch mainly at night, are collected by a larval trap (Fig. 1e) which separates the adults from larvae and thus reduces cannibalism. The trap consists of a Durapipe 'T' piece, with the ends covered with 0.5 mm nylon mesh, fixed into the side of a 800 ml cylindrical plastic container. These containers, holding a hatch from the previous night, can be lifted from the system and larvae then transferred to either individual or mass culture containers. The adult-holding tanks and larval traps are all placed in a shallow tray (Fig. 1f) which collects spillages and drains into the filter system beneath. The main return from the larval traps is piped direct to the filter to minimize evaporation.

The filter consists of a synthetic fibre (Fig. 1g) to remove any detritus in the circulating water; this part of the filter is replaced every week. The sea water then passes through a biological filter comprising a plastic cylinder (38 cm high × 18 cm diameter) filled with crushed mussel shell. Bacteria in this filter remove complex organic molecules produced by the animals in the system. Samples of water from the top and bottom of the filtering column tested for ammonia, nitrite and nitrate content show that complete nitrification is occurring. Before prawns are placed in the holding tanks, the circulation system is run for 4 weeks at 15 °C in order to build up the bacterial population on the surface of the shell material in the filter. After passing through this biological filter the sea water is collected in a large reservoir (Fig. 1i) (50 × 55 × 90 cm) capable of holding all the water in the system should the pump fail. A valve (Fig. 1j) isolates the pump from the main reservoir so that bearing maintenance can be carried out at regular intervals, usually every 12 months. A Totton Electrical Sales Ltd pump (Model 175B/M/DP) with a ceramic impeller delivers water at 720 l/h to the header tank through a specially designed ultra-violet (UV) filter which helps to limit the build-up of bacteria and fungi in the system. The UV unit consists of a light alloy hexagonal outer case, diameter 20 cm (Fig. 1l) surrounding a 1 m length of quartz tubing (Fig. 1m) of 4 cm internal diameter (ID) which connects by 'O' ring adaptors to the 2 cm ID Durapipe at each end. Fixed inside the casing are six Phillips 90 cm UV tubes (Fig. 1n) at a distance of 4 cm from the quartz tube.

Over-flow from the header tank passes through two pipes (Fig. 1o) and is splashed into the reservoir to give effective aeration. A further emergency overflow (Fig. 1p) connects through the trough 'f' to the reservoir. The entire circulation system contains 220 l of sea water, of which 25 l are replaced every 14 days.

'Water quality' (specific gravity, salinity, pH and water temperature) was monitored every 2–3 days from October 1974 to October 1975. Once the system had stabilized after an initial 4 week run-in period these factors remained relatively stable: S.G. 1.026, standard deviation (s.d.) 0.002; salinity 40.1, s.d. 2.7‰; pH 8.07, s.d. 0.18; temperature 17.1, s.d. 0.9 °C. The Electronic Switchgear salinometer was checked as part of an experiment run by the International Council for the Exploration of the Sea (I.C.E.S.) and our readings of 7.976‰ (low salinity Baltic sample) and 38.123‰ (Mediterranean sample) were acceptably close to the means of 8.011‰ and 38.125‰ respectively.

Larval culture

Two methods of culture were used, mass and individual, and in both water and food were changed every 2–3 days. In mass cultures up to 100 larvae were placed in plastic jars containing 1.5 l of Plymouth sea water and 0.02 mg/ml Streptomycin sulphate. This antibiotic is reported to be entirely effective in controlling bacilli introduced with the cultured *Artemia* nauplii used as food (Gilmour *et al.*, 1975). Gentle aeration was provided through a sintered glass block to keep both the larvae and *Artemia* circulating. *Artemia* eggs were hatched in 2 l of sea water with antibiotic in glass jars, and aerated vigorously for 48 h in an incubator at 25 °C. Five millilitres of newly hatched, concentrated nauplii were fed to the mass culture at each water change. To change the water the contents of the mass culture jar were poured gently through a 0.5 mm nylon mesh to retain the larvae which were then washed off into clean water. Each time the water was renewed, four larvae were preserved in 4% formalin.

The individual culture method used lidded trays of clear plastic with 18 compartments each of which holds 50 ml sea water with antibiotic. Two drops of concentrated *Artemia* nauplii were added, increasing to four drops as the larvae increased in size. The trays were examined every 2–3 days and any deaths or moults were recorded. Moults were pipetted out and preserved in formalin for subsequent examination.

Dissections were made in a 1 : 1 mixture of glycerine and 4% formalin under a Wild M5 microscope; a Wild M20 with camera lucida and phase contrast was used for drawings. Measurements of whole larvae were made from the tip of the rostrum to the base of the spines on the telson. In order to study morphological variation, especially of setal counts, flagellar segmentation and length ratios, all available material was examined at each zoeal stage. This included those larvae preserved regularly from mass cultures and all moults retained from the individual cultures. For each of the early zoeal stages up to 60 larvae and moults were examined and in later stages, even with mortality, at least 10 were examined.

Palaemon (Paleander) elegans Rathke, 1837

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Leander squilla Czerniavsky, 1884.

Leander squilla elegans De Man, 1915.

Leander squilla intermedia De Man, 1915.

Leander squilla typica De Man, 1915.

Palaemon (Paleander) elegans Holthuis, 1950.

SYNOPSIS OF LARVAL DATA FROM PUBLISHED WORK. *Leander squilla* Stuxberg, 1874 (zoea 1, plankton, Swedish waters); *Leander squilla* Keeble & Gamble, 1904 (zoea 1, chromatophores); *Leander squilla* Gurney 1924 (zoeae 1, 2 laboratory reared, not zoea 5 = post-larva, plankton, British waters); *Leander squilla elegans* Wimpenny & Titterington, 1936 (zoeae 1–6, post-larva, plankton, Lake Qarun, Egypt); *Leander squilla typica* Høglund, 1943 (zoeae 1–6, post-larvae, plankton and laboratory reared, Swedish waters); *Palaemon elegans elegans* Tsurnamal, 1963 (zoeae 1–8, post-larva, laboratory reared, Israeli waters); *Palaemon elegans* Rochanaburanon & Williamson, 1976 (zoeae 1–9, post-larvae, laboratory reared, British waters).

In this paper, larvae employing thoracic appendage propulsion will be described as zoeae. Individuals using abdominal (pleopod) propulsion will be described as post-larvae and later, as juveniles, when all characters except secondary sexual characters of the adult are present (Williamson, 1969). In the following short descriptions of the key characters of the larval stages, all setal counts have been omitted but these are recorded in Table 2.

DESCRIPTION OF LARVAL STAGES.

Key characters are printed in *italic type*.

ZOEA 1 (Fig. 2) 3.1 mm (2.8–3.2 mm)

Head (Figs 2a, b): *eyes sessile*.

Carapace (Figs 2a, b): *without spines, rostrum straight*, tapering distally, ventral margin with minute retrorse teeth distally.

Antenna 1 (Fig. 2c): peduncle bearing single flagellar segment with two aesthetascs distally.

Antenna 2 (Fig. 2d): exopodite (scaphocerite or antennal scale) as a broad lamina divided into four short segments distally.

Maxillipeds 1–3 (Figs 2h–j): with natatory exopodites.

Pereiopods 1, 2 (Figs 2k, l): *rudimentary, biramous*. No trace of pereiopods 3–5.

Abdomen (Figs 2a, b): somite 5 with posterior margin produced into a pair of short spines, *somite 6 continuous with telson*. No trace of pleopods.

Telson (Fig. 2m): fans out distally, posterior margin bears 7+7 plumose spines, with minute spines between four innermost pairs of spines.

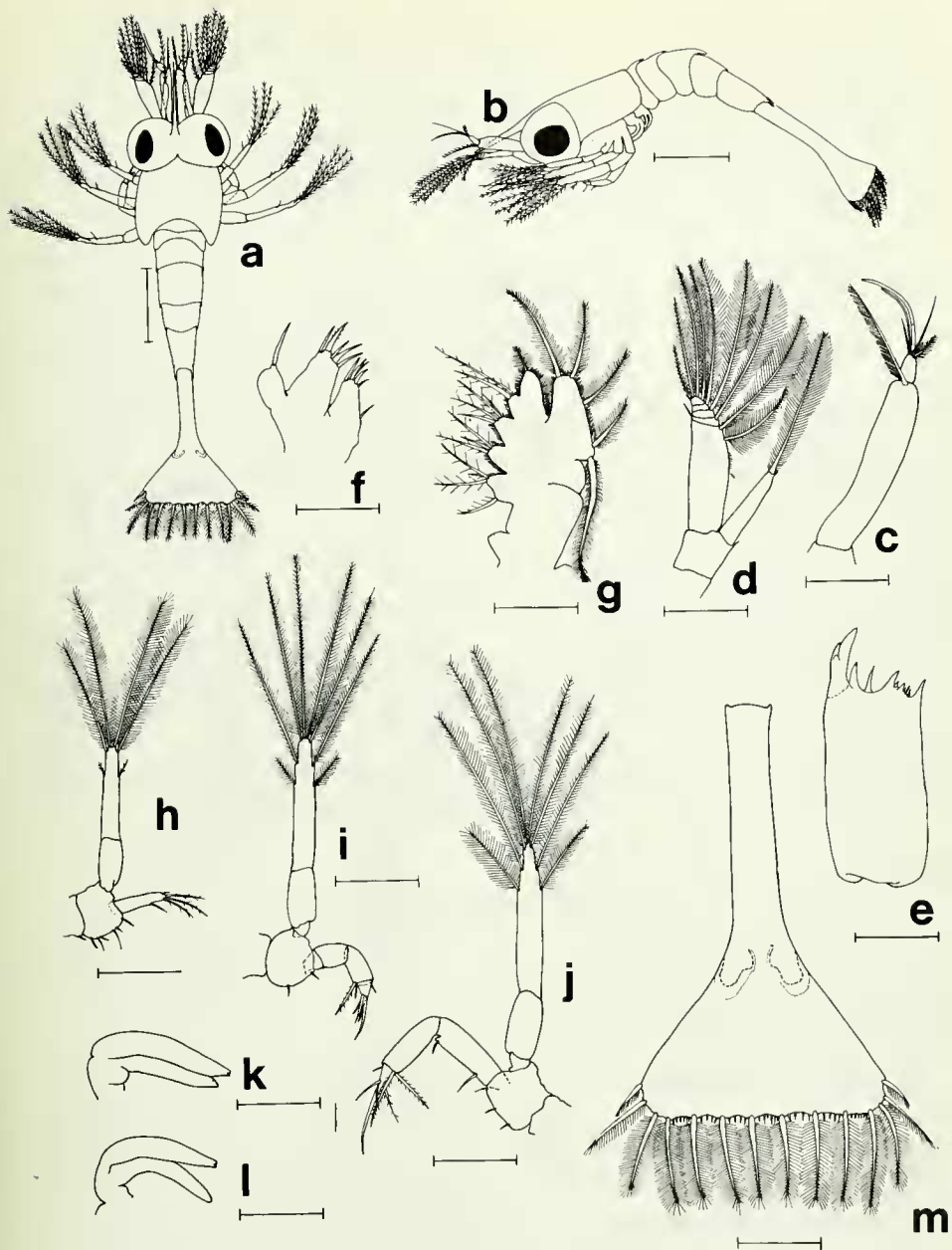


Fig. 2 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) telson. Bar scales: a, b=0.5 mm; c, d, h, i, j, k, l=0.2 mm; g=0.1 mm; e, f=0.05 mm.

ZOEA 2 (Fig. 3) 3.2 mm (3.0–3.4 mm)

Head (Figs 3a, b): *eyes 'stalked'*.

Carapace (Figs 3a, b): *one dorso-medial and a pair of supraorbital spines* all bent forward with small retrorse teeth ventrally, *rostrum without teeth, downturned at end to form small hook*.

Pereiopods 1, 2 (Figs 3l, m): *developed, with natatory exopodites*.

Pereiopods 3, 4 (Figs 3n, o): *rudimentary, biramous*.

Pereiopod 5 (Fig. 3p): *rudimentary, uniramous* (without exopodite).

Telson (Fig. 3q): *developing uropods visible beneath exoskeleton*; in central group of small spines, one pair longer than the others.

ZOEA 3 (Fig. 4) 3.6 mm (3.3–3.8 mm)

Carapace (Figs 4a, b): *two dorso-medial spines* and a pair small frontolateral spines at edge of carapace beneath eyes, former with retrorse teeth ventrally.

Antenna 1 (Fig. 4c): conspicuous spine medially and stylocerite forming on proximal external margin of first segment of peduncle; distal segment of peduncle bearing first segment of internal flagellum.

Antenna 2 (Fig. 4d): exopodite with distal part divided into only two short segments.

Abdomen (Figs 4a, b): *somite six divided from telson by suture*.

Telson (Fig. 4p): narrower but still broader distally, outer pair of spines on posterior margin considerably reduced, *uropod endopodite with no marginal setae, exopodite with marginal plumose setae*.

ZOEA 4 (Figs 5, 6) 3.8 mm (3.4–4.1 mm)

Carapace (Figs 5a, b): *three dorso-medial spines* with small retrorse teeth ventrally, rostrum weakly hooked at apex.

Antenna 2 (Fig. 6b): endopodite three-quarters length of scaphocerite, distal part of exopodite no longer divided into short segments but with a stout, terminal spine on outer, distal edge.

Pereiopod 3 (Fig. 6h): *developed, with natatory exopodite*.

Pereiopod 4 (Fig. 6i): *rudimentary, biramous*.

Pereiopod 5 (Fig. 6j): *developed, uniramous*.

Telson (Fig. 6k): a little broader distally than proximally, posterior margin concave with 4+4 spines, *endopodite and exopodite of uropod both with marginal plumose setae*.

ZOEA 5 (Figs 7, 8) 4.5 mm (4.2–4.8 mm)

Antenna 1 (Fig. 7c): external flagellum with four distal aesthetascs.

Antenna 2 (Fig. 7d): endopodite with two-segmented flagellum, four-fifths length of scaphocerite (excluding setae).

Pereiopods 1, 2 (Figs 8d, e): *endopodite with internal distal margin of propodus produced slightly forward* (will become immobile finger of chela).

Pereiopod 4 (Fig. 8g): *developed, with natatory exopodite*.

Abdomen (Figs 7a, b): *somites 1–5 with rudimentary pleopods*.

Telson (Fig. 8i): subquadrate, posterior margin weakly concave.

ZOEA 6 (Figs 9, 10, 11) 5.2 mm (4.8–5.5 mm)

Carapace (Fig. 9b): *short plumose seta in angle of anterior dorso-medial spine*, rostrum straight or weakly hooked.

Antenna 2 (Fig. 9d): endopodite with three-segmented flagellum.

Pereiopods 1, 2 (Figs 10d, e): *endopodite with internal distal margin of propodus produced forward to over half length of dactylus* (excluding terminal setae).

Abdomen (Figs 9b, 10i–m): *pleopods on somites 1–5 rudimentary, biramous*.

Telson (Fig. 11a): wider medially than distally, posterior margin length about one-third overall length of telson.

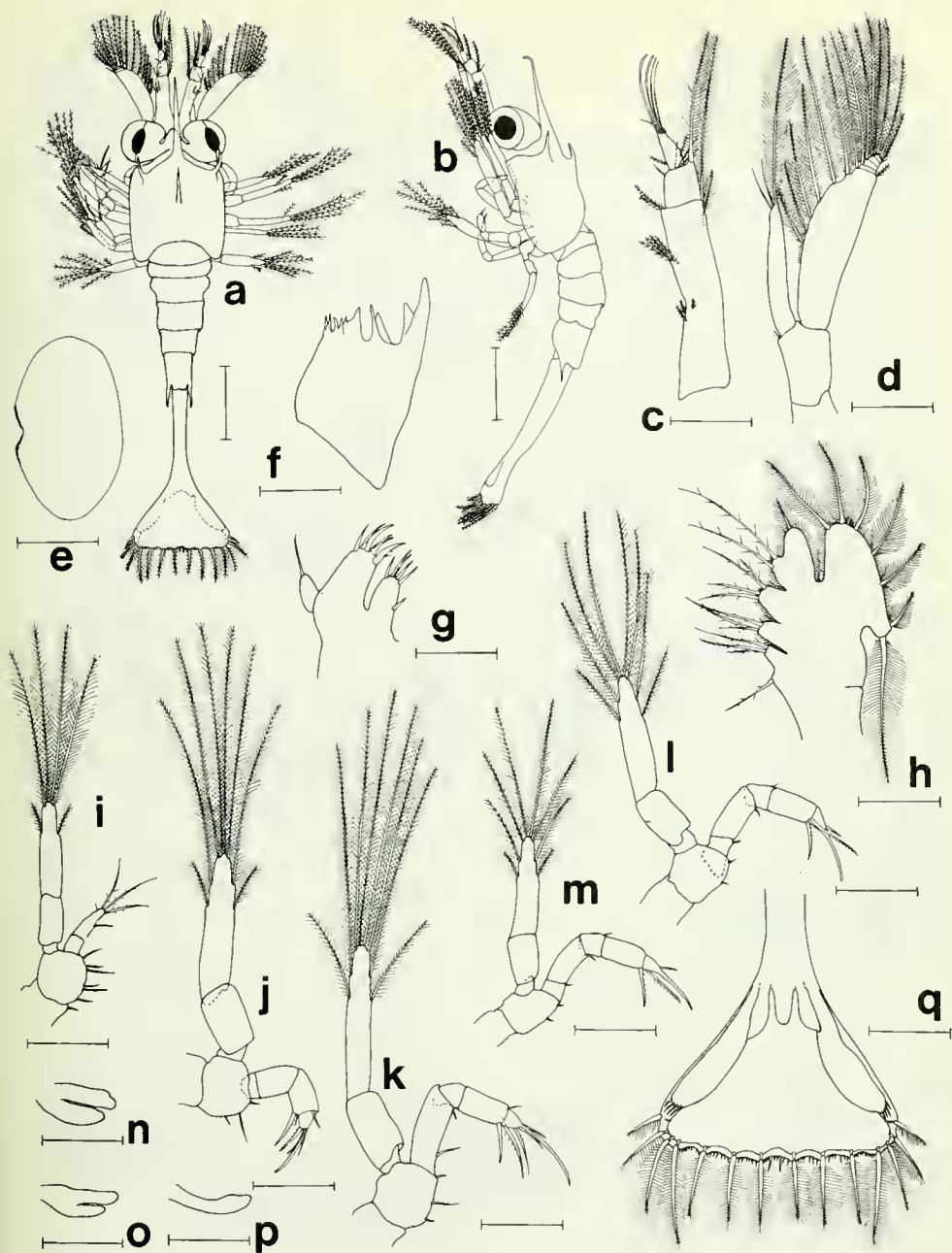


Fig. 3 Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) upperlip (labrum); (f) mandible; (g) maxilla 1; (h) maxilla 2; (i) maxilliped 1; (j) maxilliped 2; (k) maxilliped 3; (l) pereiopod 1; (m) pereiopod 2; (n) pereiopod 3; (o) pereiopod 4; (p) pereiopod 5; (q) telson. Bar scales: a, b = 0.5 mm; c, d, i, j, k, l, m, n, o, p, q = 0.2 mm; e, g, h = 0.1 mm; f = 0.05 mm.

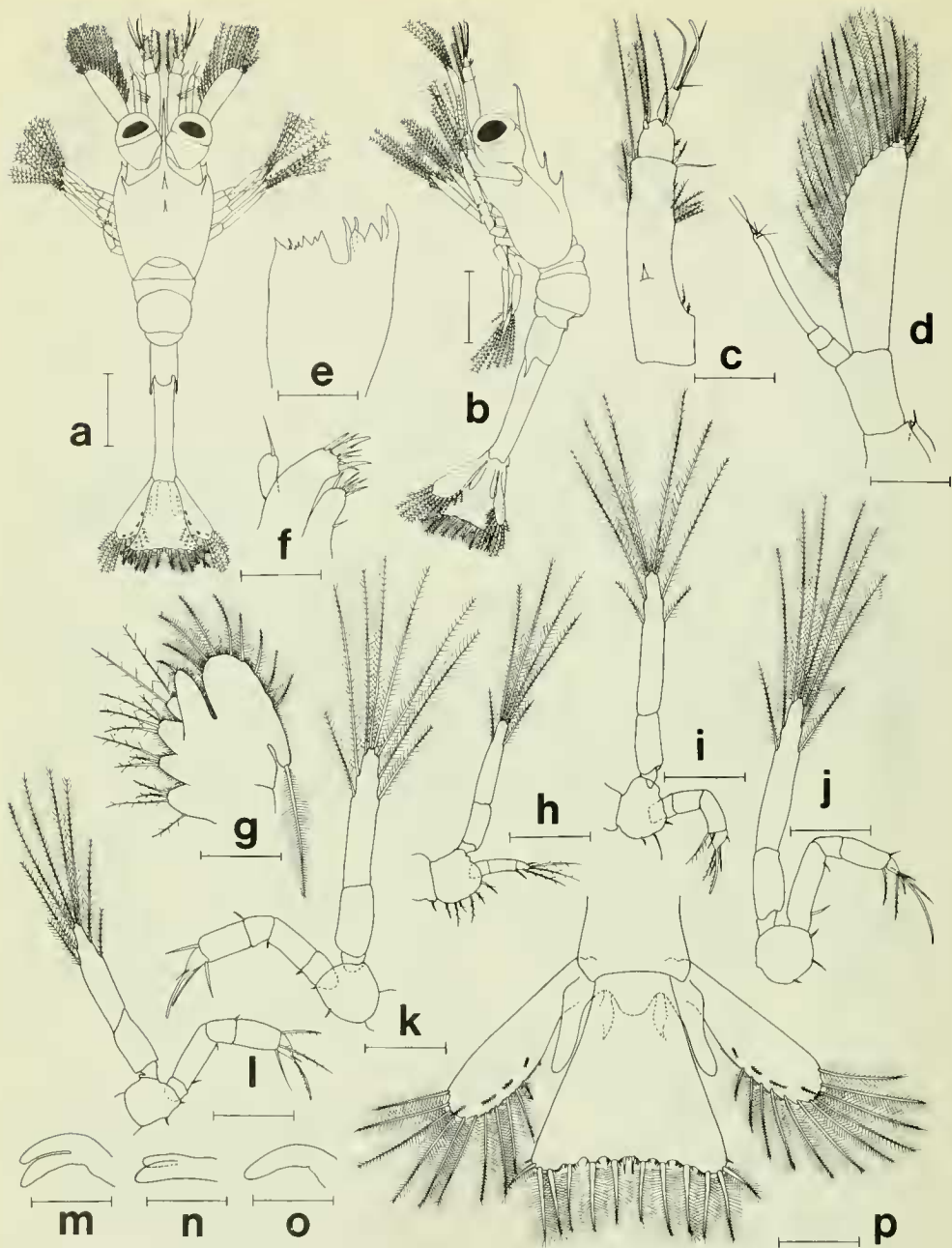


Fig. 4. Zoea 3: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0.5 mm; c, d, h, i, j, k, l, m, n, o, p = 0.2 mm; f, g = 0.1 mm; e = 0.05 mm.

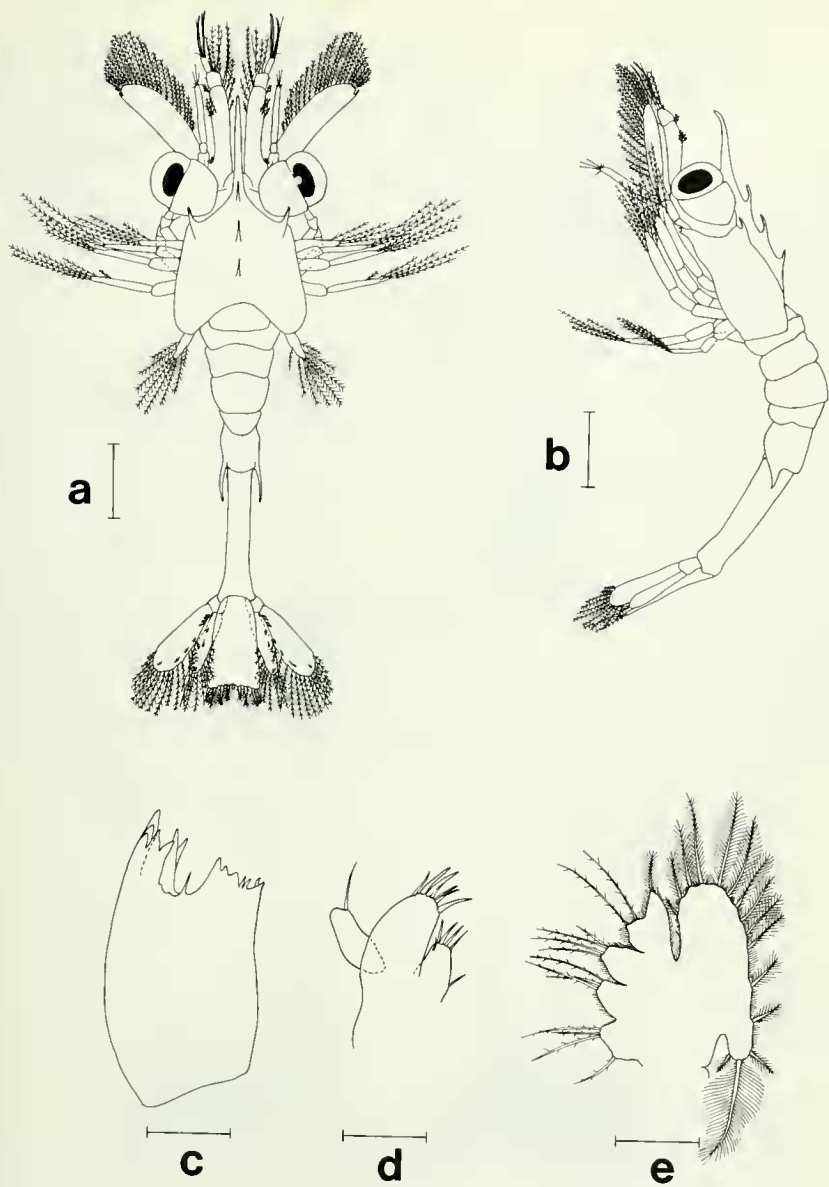


Fig. 5 Zoea 4: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2.
Bar scales: a, b=0.5 mm; c=0.05 mm; d, e=0.1 mm.

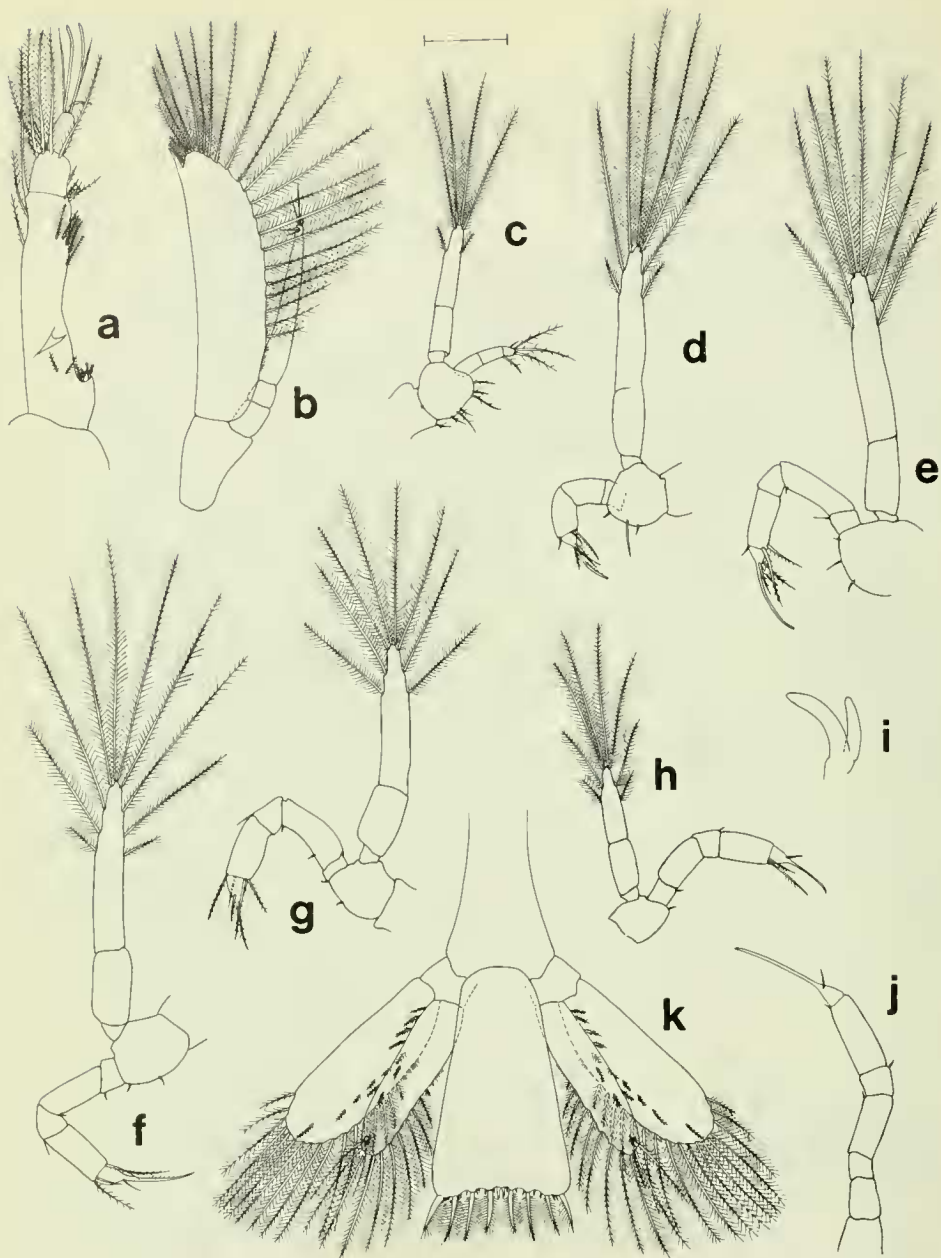


Fig. 6 Zoea 4: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) telson. Bar scale: a-k=0.2 mm.

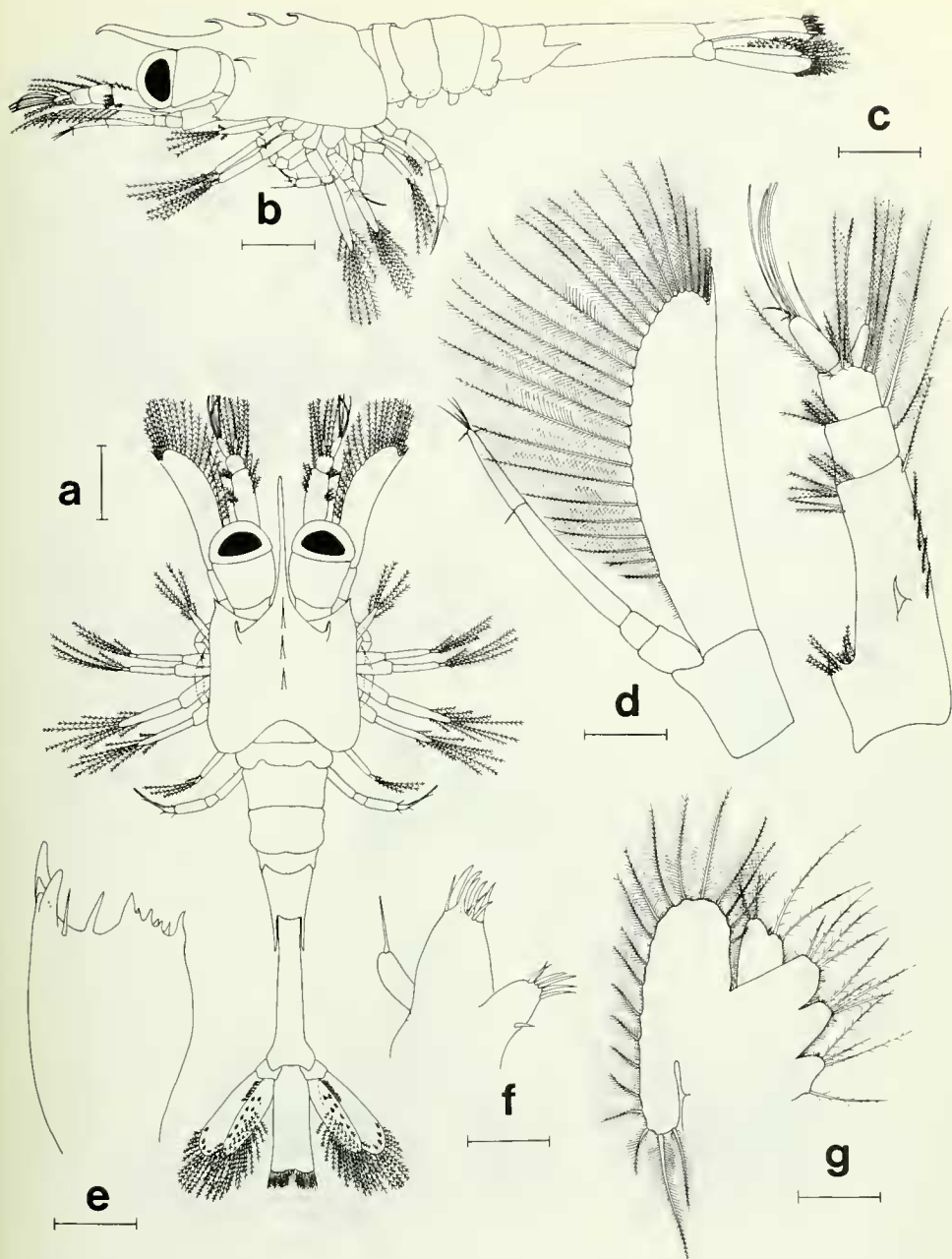


Fig. 7. *Zoea* 5: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b=0.5 mm; c, d=0.2 mm; e=0.05 mm; f, g=0.1 mm.

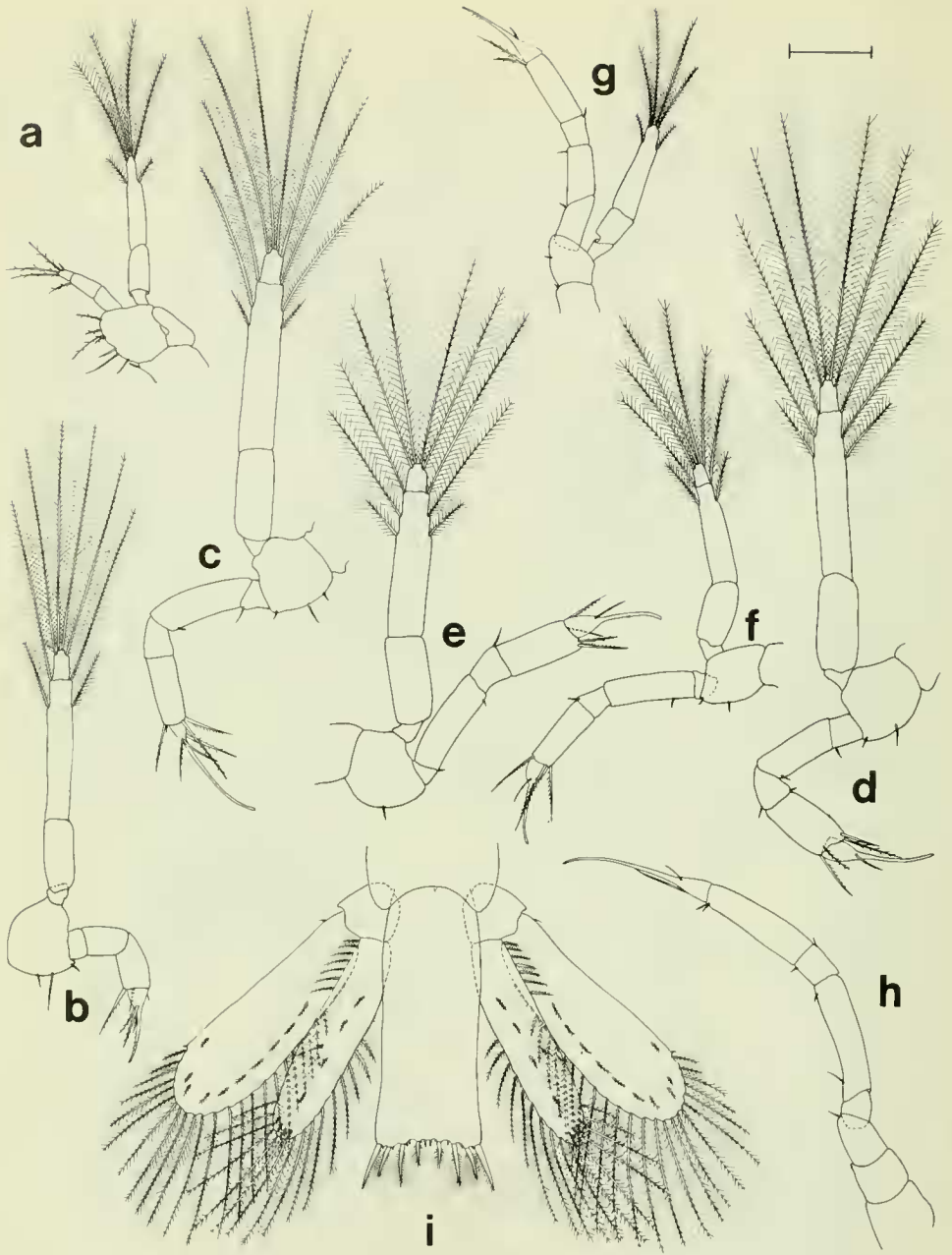


Fig. 8 Zoea 5: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopod 2; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5; (i) telson. Bar scale: a-i=0.2 mm.

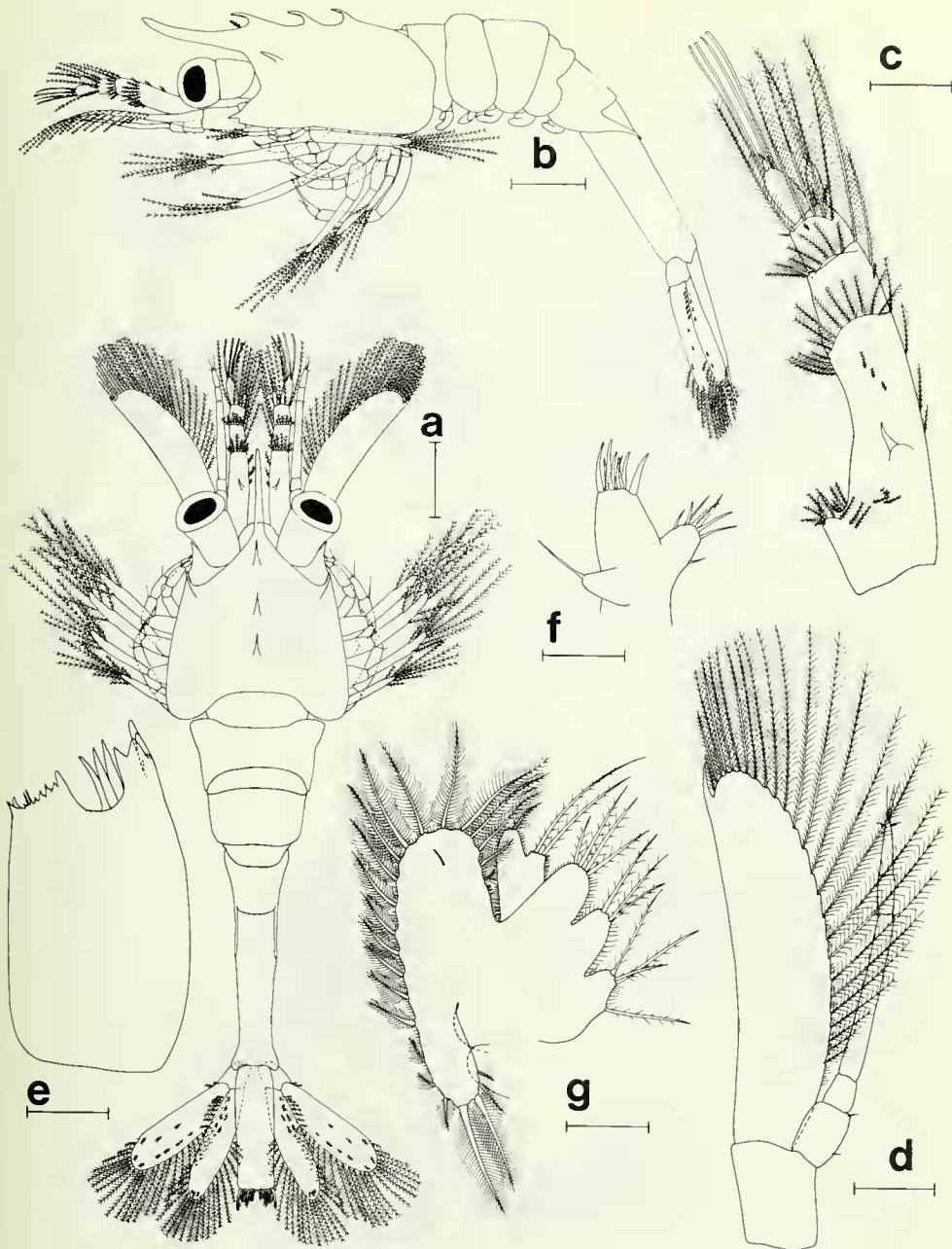


Fig. 9 Zoea 6: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b=0.5 mm; c, d=0.2 mm; e=0.05 mm; f, g=0.1 mm.

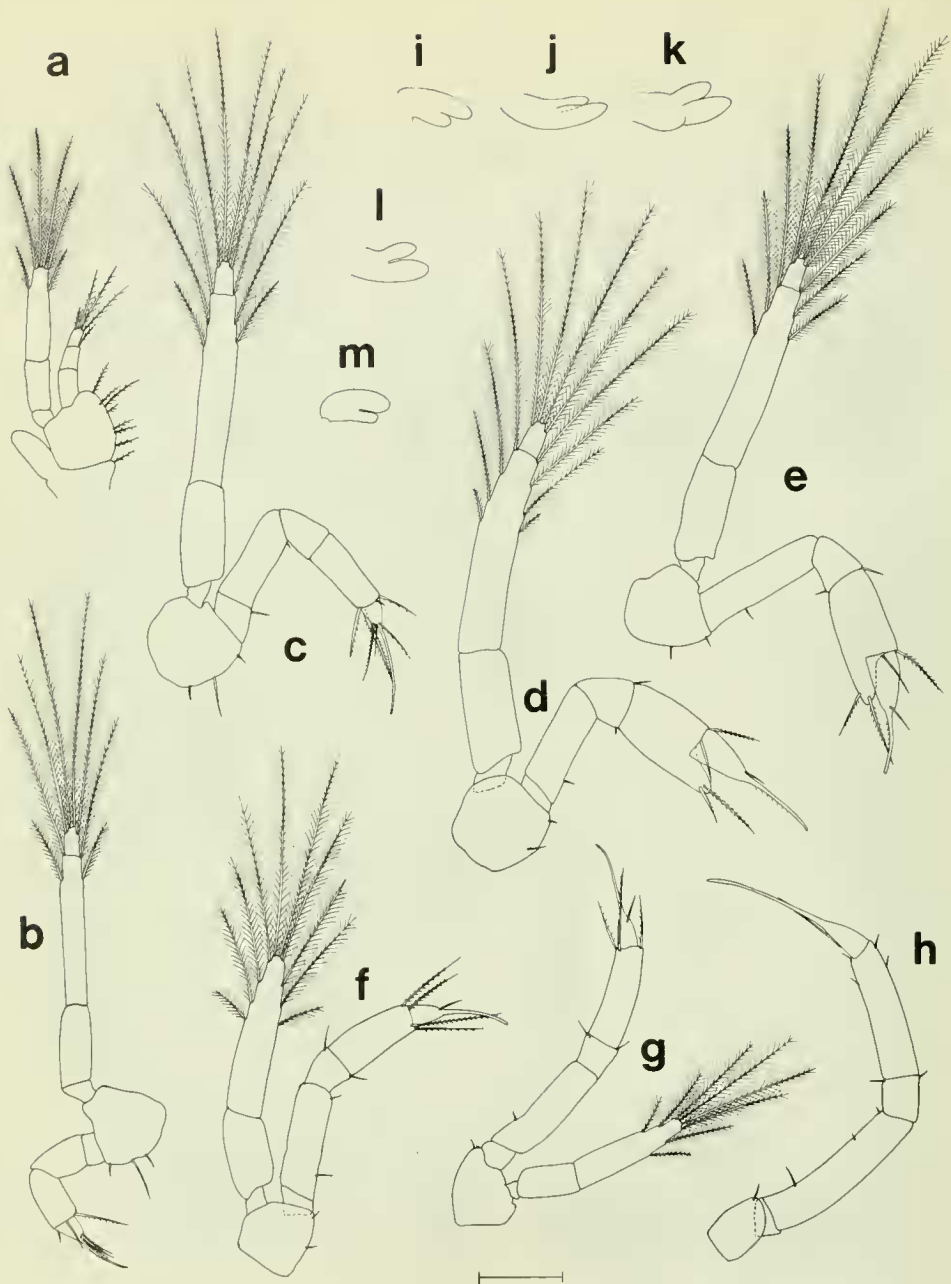


Fig. 10 Zoea 6: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereopod 1; (e) pereopod 2; (f) pereopod 3; (g) pereopod 4; (h) pereopod 5; (i) pleopod 1; (j) pleopod 2; (k) pleopod 3; (l) pleopod 4; (m) pleopod 5. Bar scale: a-m=0.2 mm.

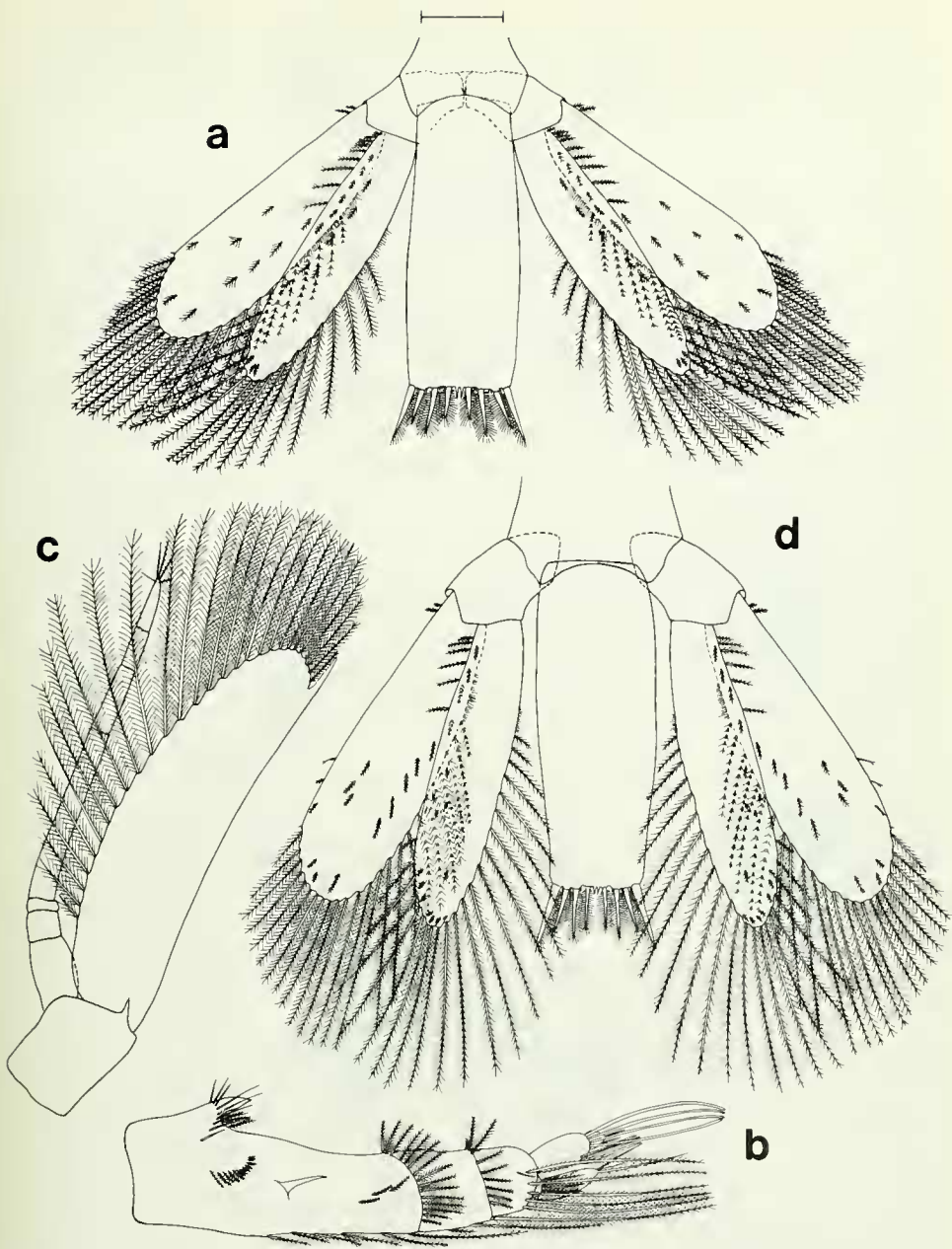


Fig. 11 Zoa 6: (a) telson. Zoa 7: (b) antenna 1; (c) antenna 2; (d) telson. Bar scale: a-d=0.2 mm.

ZOEA 7 (Fig. 11)

Similar in most characters to zoea 6 with the following exceptions:

Antenna 1 (Fig. 11b): circlet of plumose setae developed dorsally on first segment of peduncle, indicating position of statocyst, additional group of three aesthetascs on external flagellum.

Antenna 2 (Fig. 11c): *increase in number of segments of endopodite flagellum, approximately equal to scaphocerite in length.*

Telson (Fig. 11d): slightly narrower distally.

ZOEA 8 (Figs 12, 13, 14, 15) 6.4 mm (6.0–6.6 mm)

Carapace (Fig. 12b): *three short setae in angle of anterior dorso-medial spine, rostrum no longer hooked.*

Antenna 1 (Fig. 12c): external flagellum of two segments, further group of two aesthetascs added proximal to other two groups.

Antenna 2 (Fig. 13a): *flagellum of exopodite multisegmented, just longer than scaphocerite.*

Pereiopods 1, 2 (Figs 14a, b): *endopodite with immovable finger of propodus produced forward to almost length of dactylus (excluding terminal setae).*

Abdomen (Figs 12b, 13h–l): *pleopods with rudimentary setae on margins of endopodite (except pleopod 1) and exopodite, endopodite of pleopods 2–5 with rudiment of appendix interna (stylambly).*

Telson (Fig. 15a): narrowing distally, *posterior margin convex*, pair of small spines at distal corners.

ZOEA 9 (Figs 15, 16, 17) 7.4 mm (7.0–8.0 mm)

Carapace (Fig. 16b): *five setae in angle of anterior dorso-medial spine.*

Antenna 1 (Fig. 15c): internal flagellum of three segments, additional group of two aesthetascs proximally on first segment of external flagellum.

Antenna 2 (Fig. 15d): *endopodite with flagellum approximately 1.5 times length of scaphocerite.*

Abdomen (Figs 17g–k): *pleopods with some plumose setae on margins of exopodites.*

Telson (Fig. 15b): further narrowing distally, *no small spines between large spines.*

POST-LARVA 1 (Figs 18, 19, 20) 7.9 mm (7.5–8.4 mm)

Carapace (Fig. 19a): *rostrum usually with eight (7–9) dorsal and two ventral spines, supraorbital spines missing.*

Antenna 2 (Fig. 18b): *endopodite twice length of scaphocerite, about 27 segments.*

Mandible (Fig. 18c): *divided into pars incisiva and pars molaris, lacinia mobilis no longer present and palp (two-jointed in adult) not yet appeared.*

Maxilliped 2 (Fig. 19c): endopodite with dactylus and merus flattened, *exopodite shortened and with no setae.*

Maxilliped 3 (Fig. 20d): endopodite dactylus shortened, *exopodite reduced* to less than the length of ischium and merus of endopodite, and without setae.

Pereiopod 1 (Fig. 19e): merus and carpus lengthened, *exopodite reduced* (less than length of basis and ischium) with a few degenerate plumose setae.

Pereiopod 2 (Fig. 19f): as for pereiopod 1 except *exopodite reduced* to about length of the basis and no setae.

Pereiopods 3, 4 (Figs 19g, h): endopodite dactylus shortened, merus carpus and propodus lengthened, *exopodite reduced*, extending half-way along ischium of endopodite and with no setae.

Pereiopod 5 (Fig. 19i): shortening of dactylus, all other segments of endopodite lengthened.

Pleopod 1 (Fig. 20a): ratio of endopodite to exopodite 1 : 4.5, *endopodite bearing terminal plumose setae, exopodite fringed with long plumose setae.*

Pleopods 2–5 (Figs 20b–e): endopodite over half the length of exopodite both with long, marginal, plumose setae, endopodite with appendix interna bearing well-developed intero-distal coupling hooks.

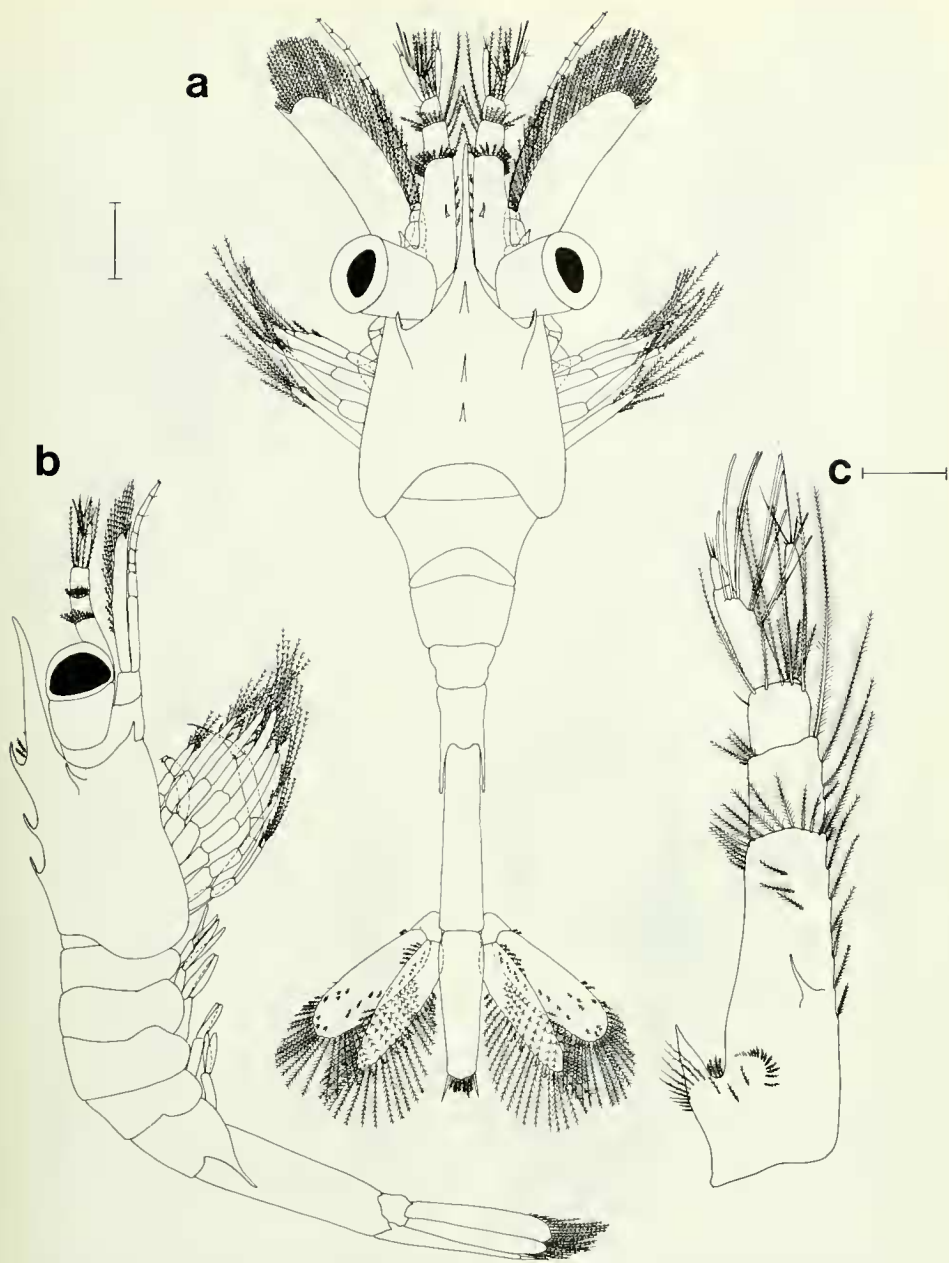


Fig. 12 Zoea 8: (a) dorsal view; (b) lateral view; (c) antenna I. Bar scales: a, b=0.5 mm; c=0.2 mm.

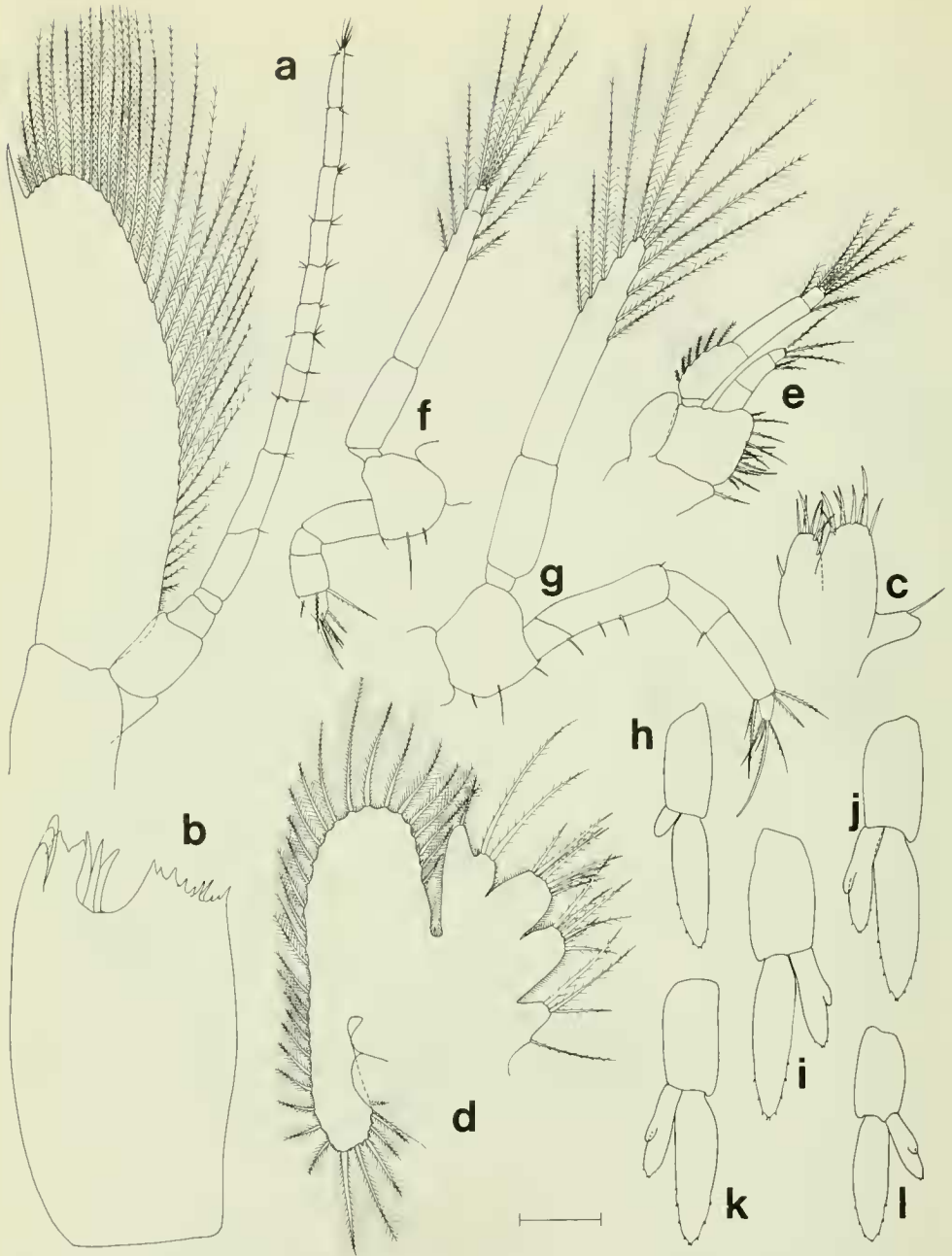


Fig. 13 Zoea 8: (a) antenna 2; (b) mandible; (c) maxilla 1; (d) maxilla 2; (e) maxilliped 1; (f) maxilliped 2; (g) maxilliped 3; (h) pleopod 1; (i) pleopod 2; (j) pleopod 3; (k) pleopod 4; (l) pleopod 5. Bar scale: a, e-l=0.2 mm; b=0.05 mm; c, d=0.1 mm.

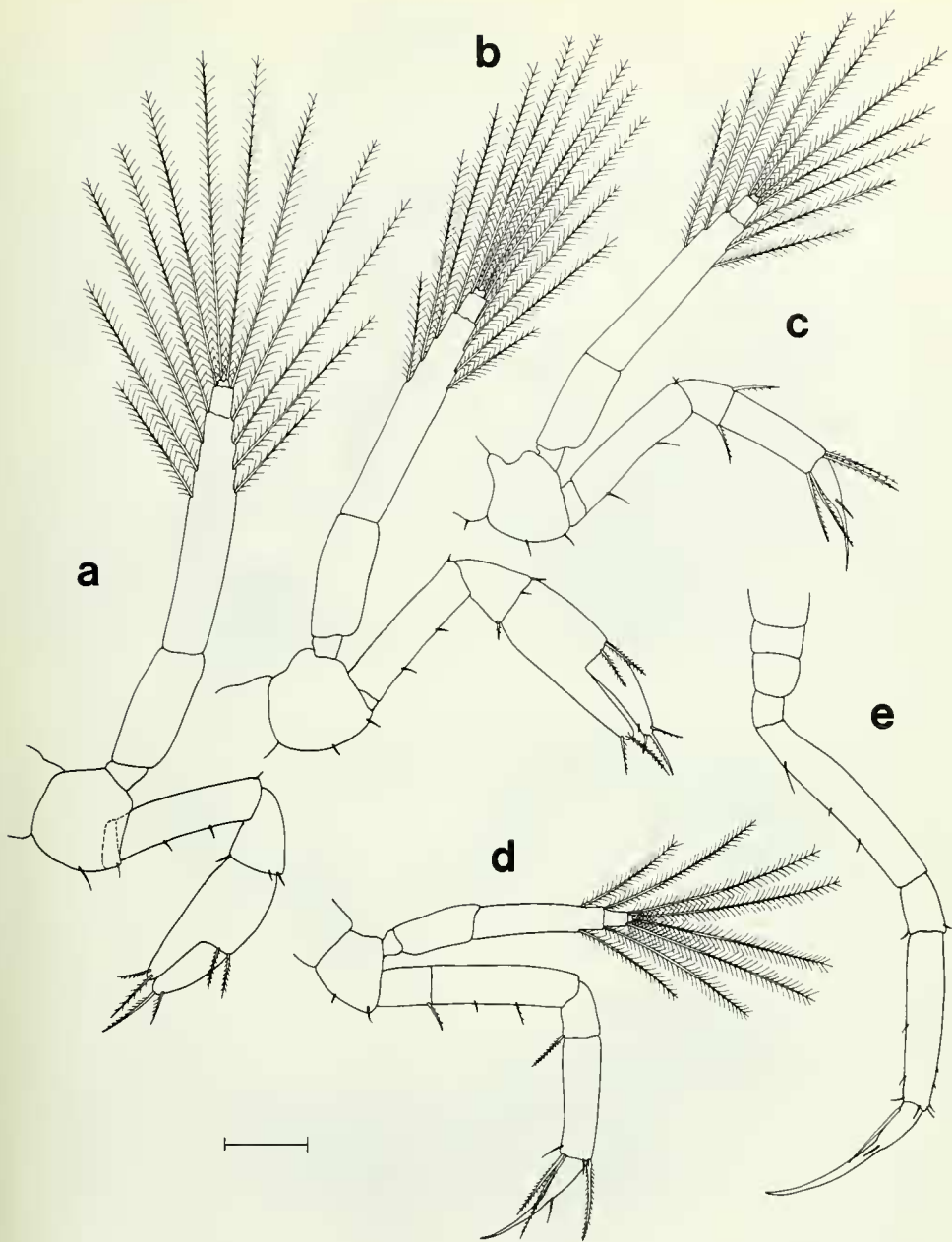


Fig. 14 Zoea 8: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5.
Bar scale: a-e=0.2 mm.

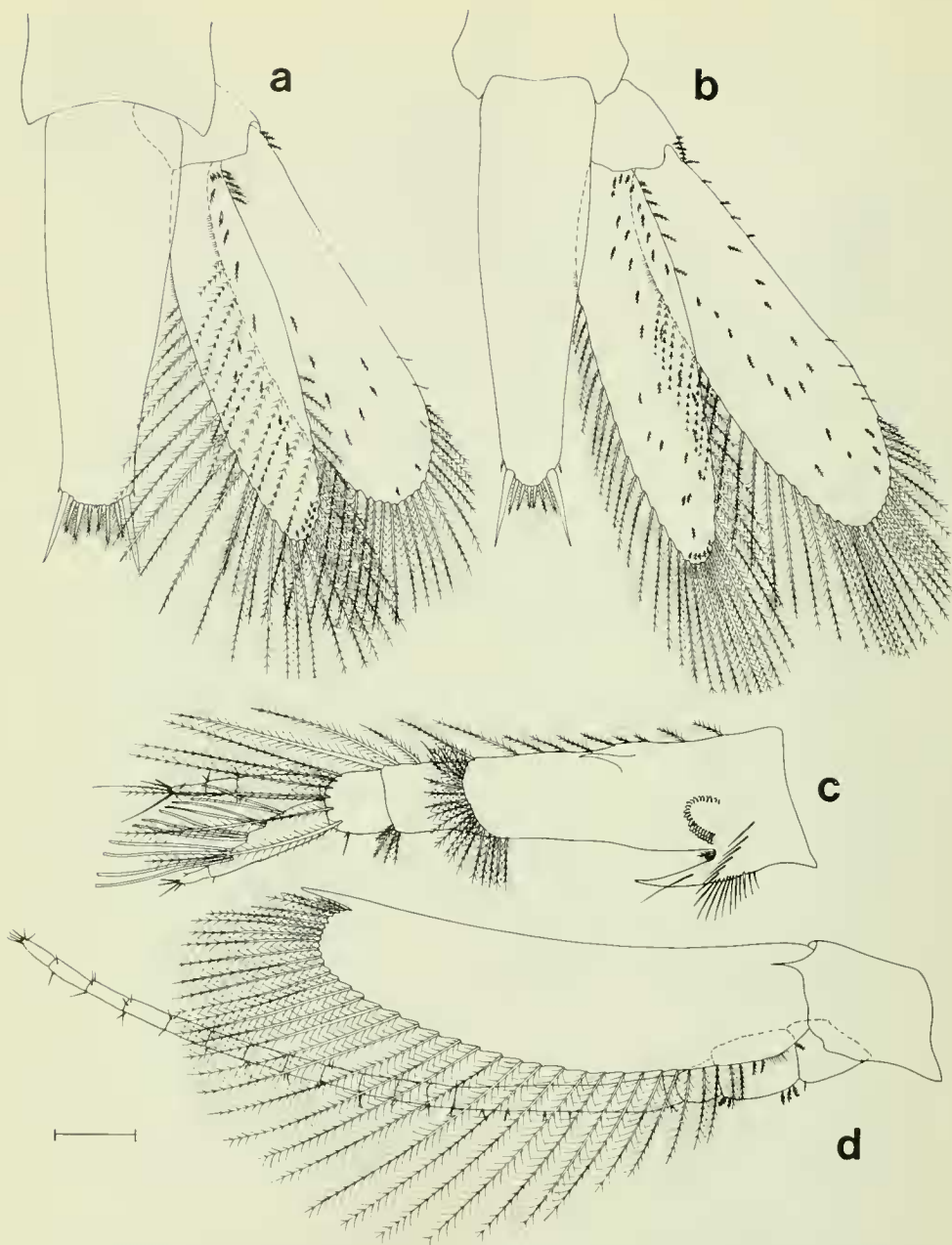


Fig. 15 Zoa 8: (a) telson. Zoa 8; (b) telson; (c) antenna 1; (d) antenna 2. Bar scale: a-d = 0.2 mm.

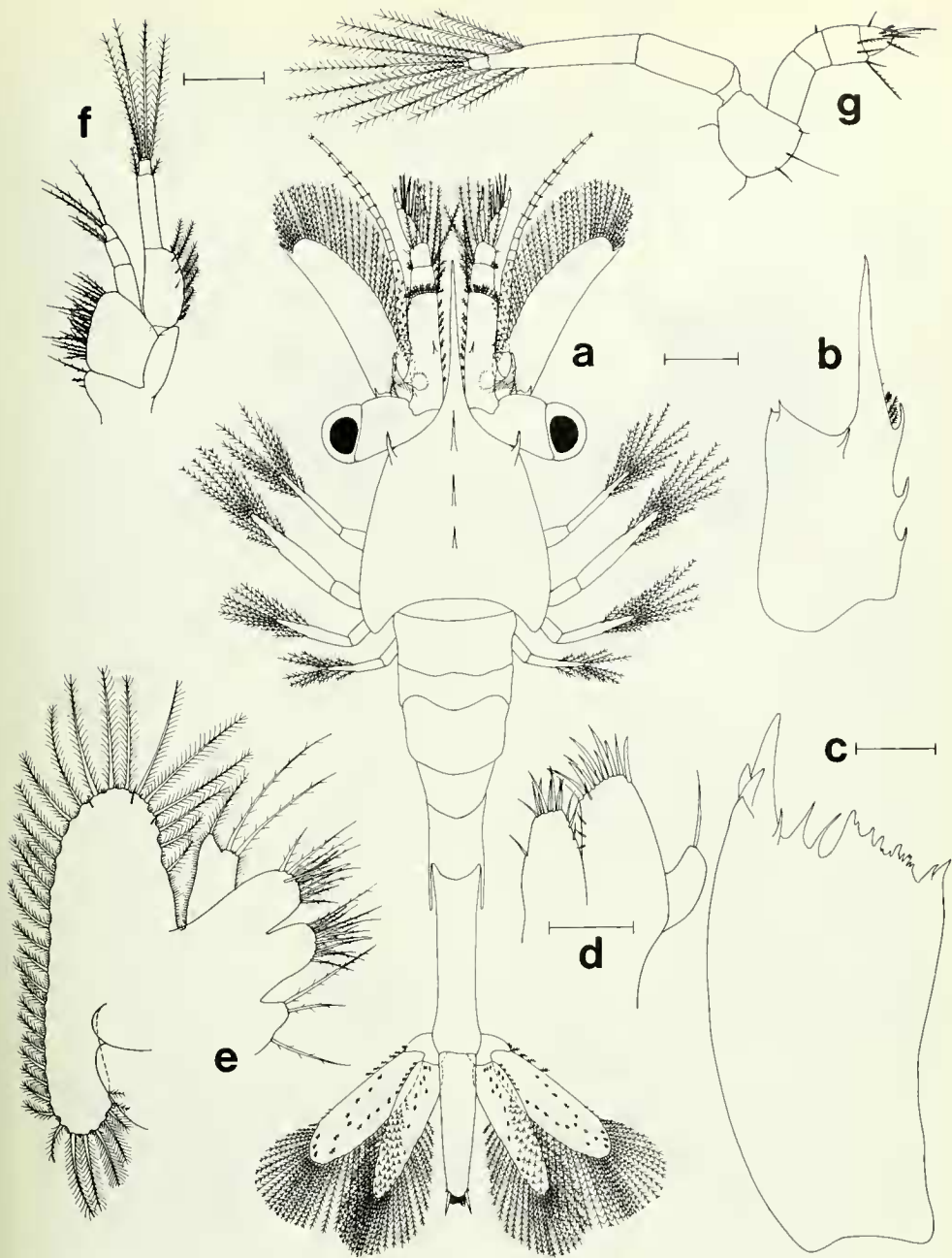


Fig. 16 Zoea 9: (a) dorsal view; (b) lateral view of carapace; (c) mandible; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2. Bar scales: a, b = 0.5 mm; c = 0.05 mm; d, e = 0.1 mm; f, g = 0.2 mm.

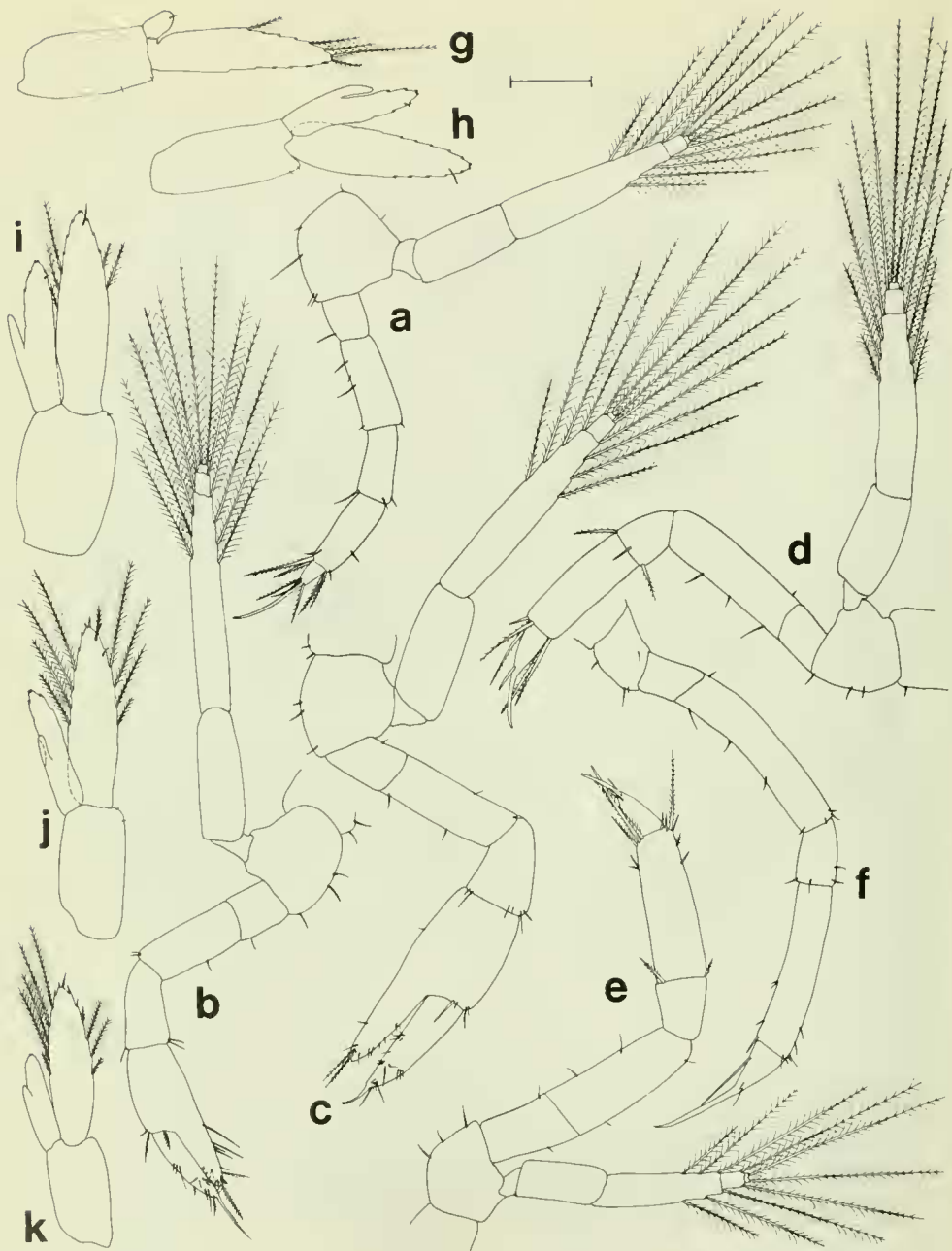


Fig. 17 Zoea 9: (a) maxilliped 3; (b) pereiopod 1; (c) pereiopod 2; (d) pereiopod 3; (e) pereiopod 4; (f) pereiopod 5; (g) pleopod 1; (h) pleopod 2; (i) pleopod 3; (j) pleopod 4; (k) pleopod 5. Bar scale: a-k=0.2 mm.

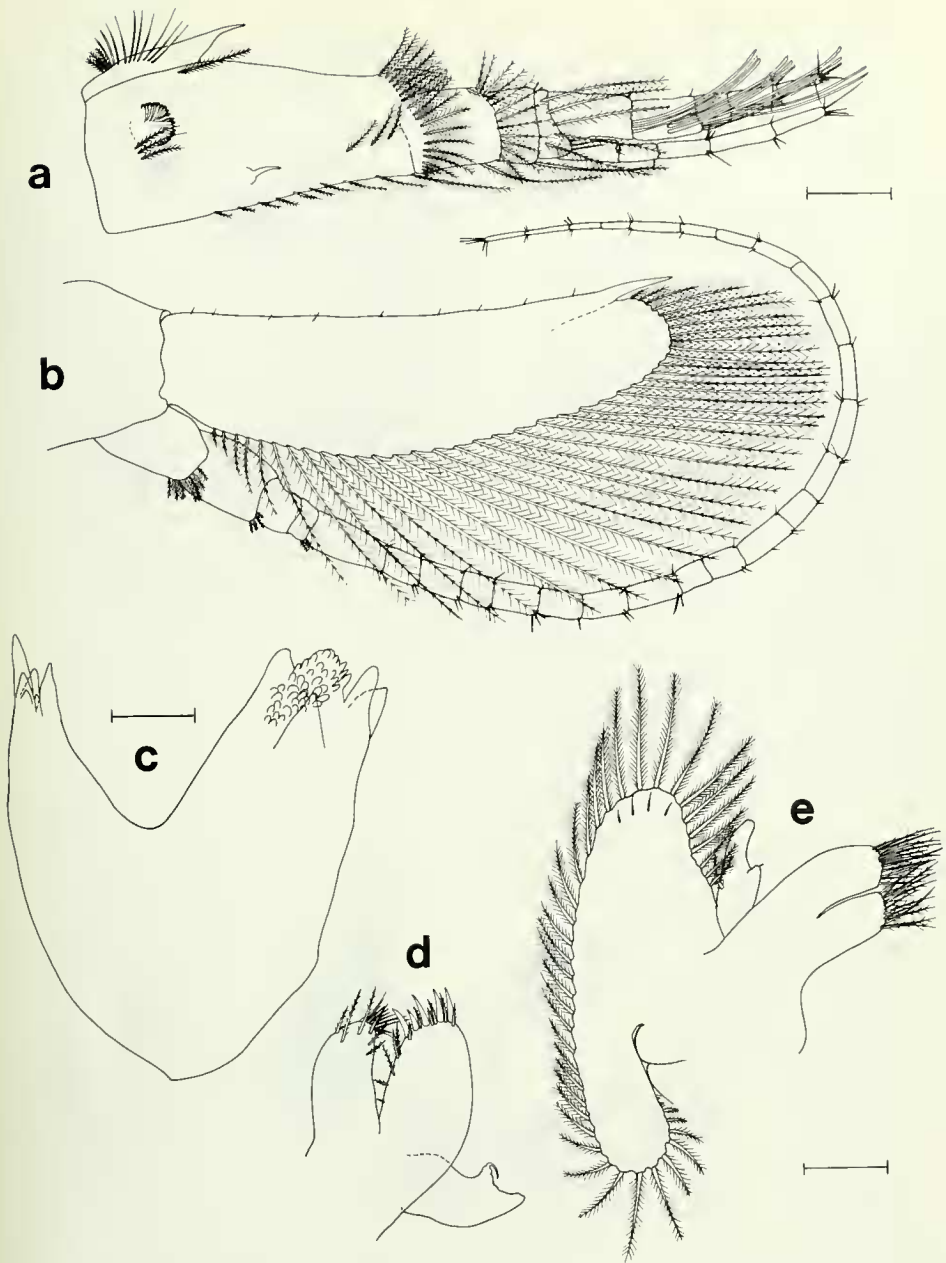


Fig. 18 Post-larva 1: (a) antenna 1; (b) antenna 2; (c) mandible; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b=0.2 mm; c=0.05 mm; d, e=0.1 mm.

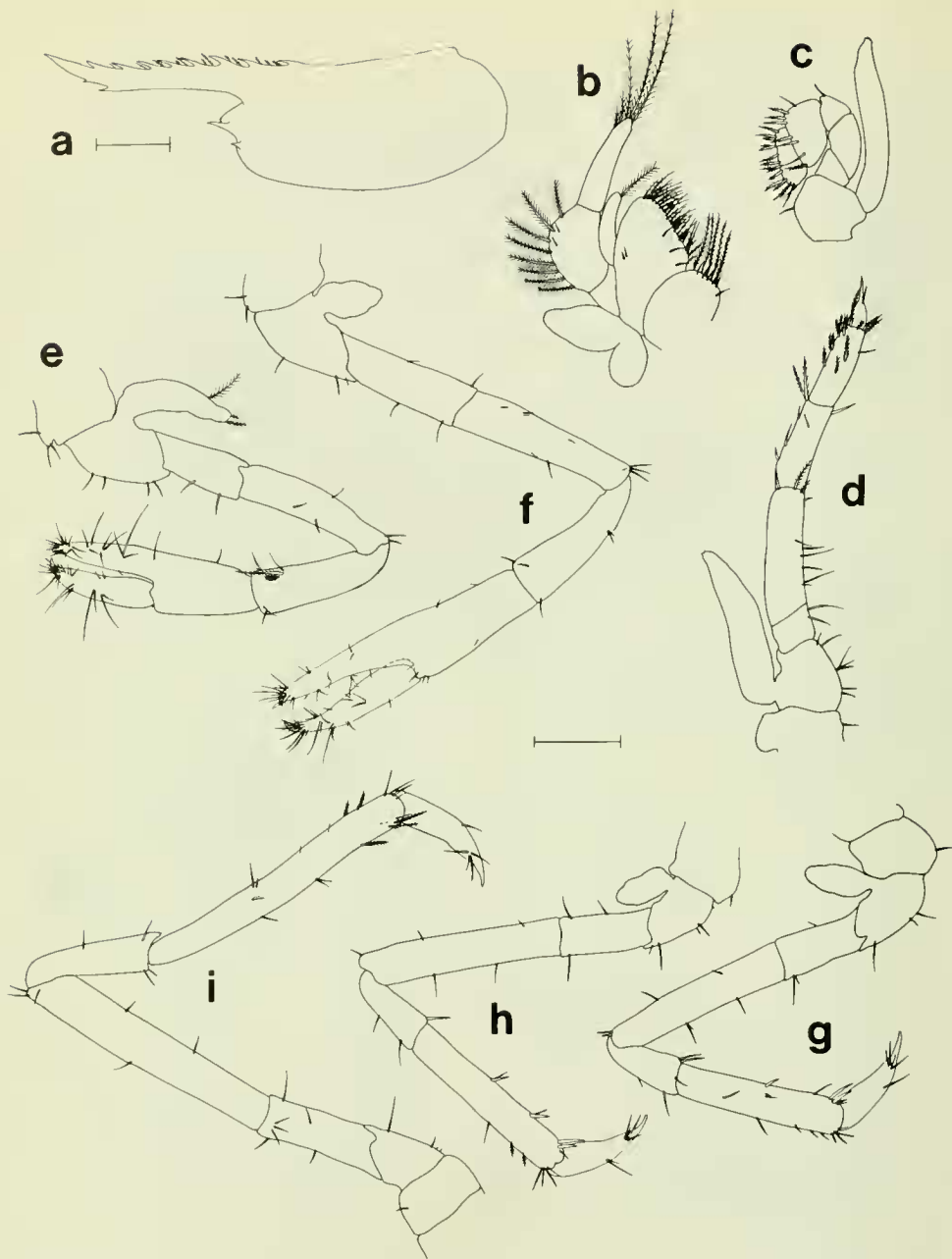


Fig. 19 Post-larva 1: (a) lateral view of carapace; (b) maxilliped 1; (c) maxilliped 2; (d) maxilliped 3; (e) pereiopod 1; (f) pereiopod 2; (g) pereiopod 3; (h) pereiopod 4; (i) pereiopod 5. Bar scales: a=0.5 mm; b-i=0.2 mm.

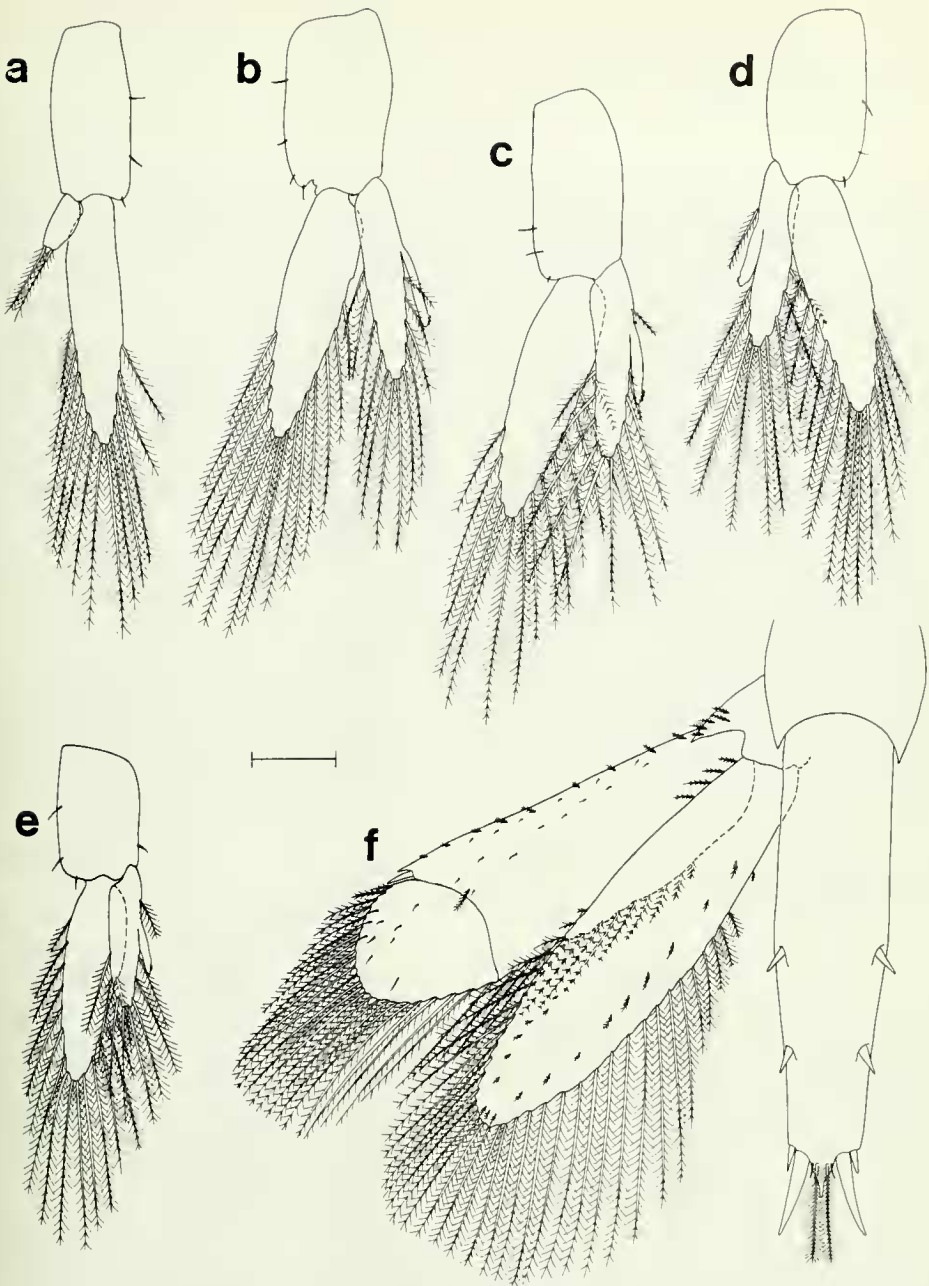


Fig. 20 Post-larva 1: (a) pleopod 1; (b) pleopod 2; (c) pleopod 3; (d) pleopod 4; (e) pleopod 5; (f) telson. Bar scale: a-f=0.2 mm.

Abdomen: *fifth abdominal somite rounded on lateral margins* and not extending to a point as in previous stages.

Telson (Fig. 20f): *extremely narrow, posterior margin tapering to a point* and bearing a pair of small (outer) and large (inner) spines and medially a pair of short, simple and a pair of plumose setae. Two pairs of stout spines developed on lateral margins of telson, *uropod exopodite divided into two parts by suture*.

Discussion

Results of previous workers and of the present study are summarized in Tables 1 and 2 from which a number of interesting points emerge. Zoeae in northern waters increase in length faster than their Mediterranean counterparts until the first post-larval stage (PL1) is reached after which the situation is reversed. One particularly interesting feature of the metamorphosis to PL1 is that the natatory exopodites of pereopods 1-4 disappear (with a stronger tendency to degeneration in the northern forms as noticed by Tsurumal, 1963). There is also a temporary regression of the exopodites of maxillipeds 2 and 3 in which the marginal plumose setae are lost and the exopodites shorten. In subsequent moults, PL1 and PL2, these plumose setae are restored and the exopodites of the maxillipeds lengthen, but the pereopods remain uniramous. It is possible that the temporary regression of exopodites of maxillipeds 2 and 3 together with other morphological changes at metamorphosis to post-larva are under the same hormone control. Hopefully, subsequent papers in this series will provide more data on these morphogenetic changes and associated modifications in swimming and feeding behaviour.

Compared with the growth of pereopods 3-5, that of pereopods 1 and 2 is remarkably rapid as the rudimentary biramous buds of these become fully formed pereopods in zoea 2 with propodus extension into fixed finger of chela beginning in zoea 4 or 5 and finally the loss of the exopodite at PL1. Uniramous pereopod 5 first appears in rudimentary form in zoea 2, before becoming 5-segmented at zoea 4; at no stage does it have an exopodite.

The changes which occur from final zoea to PL1 are dramatic and easily identifiable; the first five zoeae are also morphologically distinct. In those examples where there are only six larval stages then zoea 6 is also clearly defined. When extra moults are inserted, however, between zoeae 5 and 6, distinction between the moults is less clearly defined and considerable overlap occurs in the number of setae on appendages in successive moults. This makes the recognition of morphological stages beyond moult 5 problematical. The situation is confused by the insertion

Table 1 Lengths (mm) of zoeae and post-larvae 1 of *Palaemon (Paleander) elegans* throughout its geographical range.

Stages	Gurney, 1924 England	Wimpenny & Titterington, 1936 Egypt	Hoglund, 1943 Sweden	Tsurumal, 1963 Israel	Rochanaburanon, 1974; Rochanaburanon & Williamson ¹ , 1976 Isle of Man	Present work England
1	3.0-3.2	2.8-3.1	2.6-2.8	2.2-2.8	3.0-3.1	2.8-3.2
2	3.17-3.7	2.7-3.4	3.4-3.7	2.9-3.2	3.5-3.7	3.0-3.4
3		3.0-3.8	4.0-4.5	3.6-3.75	3.9-4.1	3.3-3.8
4		3.2-4.5	4.75-5.25	4.1-4.6	4.7-4.8	3.4-4.1
5		3.9-5.0	5.8-6.9	4.3-5.4	5.6-5.8	4.2-4.8
6		5.4-7.6	6.9-7.4	6.0-6.6	6.1-6.7	4.8-5.5
7				6.5-6.71		6.0-6.6
8				6.5-6.75		6.0-6.6
9						7.0-8.0
PL1	7.86	8.9-9.4	7.4-8.0	6.7-7.0	6.3-7.9	7.5-8.4

¹ Carapace characters PL1 not included in Table 2. Number of rostral spines: dorsal 7-9 and ventral 1-3.

Table 2 Comparison of structure in larval d

	Present work England									
	PL1	1	2	3	4	5	6	7 & 8	9	PL1
Carapace										
No. of dorsal spines	7-9	0	1	2	3	3	3	3	3	7-9
No. of ventral rostral spines	2	0	0	0	0	0	0	0	0	2
Supraorbital spines +/-	-	-	+	+	+	+	+	+	+	-
No. of antero-lateral spines	2	0	0	2	2	2	2	2	2	2
Rostrum tip - Downturned +/-	-	-	+	+	+/-	+/-	+/-	-	-	-
Ventral retrorse hooks +/-	-	+	-	-	-	-	-	-	-	-
Antenna 1										
No. of groups, Aesthetascs	3	1	1	1	1	2	3	4	4	4
Stylocerite +/-	+	-	-	+	+	+	+	+	+	+
Statocyst +/-	-	-	-	-	-	-	-	+	+	+
No. of segments, Flagellum - Internal	5-6	0	0	1	1	1	1	1	3	5
External	5	1	1	1	1	1	1	2	2	5
Accessory flagellum +/-	+	-	-	-	-	-	-	-	-	+
Antenna 2										
Endopodite - No. of segments	33	1	1	3	3	4	5	14	16	29
Length of scaphocerite	33 4.0	0.50	0.66	0.66	0.75	0.80	0.80	1.2	1.50	2.00
Exopodite - No. of distal segments	0	4	4	2	0	0	0	0	0	0
No. of plumose setae	38 35-37	9	14-16	17-20	21-22	23-26	25-29	29-34	36	36-40
External spine +/-	+	+	+	-	+	+	+	+	+	+
Mandible - Lacinia mobilis +/-	-	+	+	+	+	+	+	+	+	-
Palp +/-	-	-	-	-	-	-	-	-	-	-
Maxilla 1										
No. of endite setae - Coxa	18	6	6	6	6	7	8	8	15	17
Basis	16	5	7	7	7	8	8	8	11	16
Maxilla 2										
No. of endite setae - Coxa	0	4	4	4	4	4	4	4	3	0
Basis 1	9	4	4	4	4	4	4	7	12	12
2	9	3	3	3	3	3-4	3-4	6	12	12
Endopodite	0	2	2	2	2	2	2	2	2	0
No. of plumose setae, Exopodite	42-43	5	7	9-11	13-15	16-21	20-24	34	36	40
Maxilliped 1										
No. of setae on internal margin - Coxa	1	1	1	1	1	1	1	1	3	11
Basis	6	6	6	6	7	7	13	27	31	31
Exopodite, No. of setae - Lateral (proximal)	9 0	0	0	0	0	0	0	6	8	8
Maxilliped 2										
Endopodite - No. of segments	+	4	4	4	4	4	4	4	4	5
Exopodite +/-	-	+	+	+	+	+	+	+	+	+
Setae +/-	-	+	+	+	+	+	+	+	+	-
Maxilliped 3										
Endopodite - No. of segments	4	3	4	4	5	5	5	5	5	5
Exopodite +/-	+	+	+	+	+	+	+	+	+	+
Setae +/-	-	+	+	+	+	+	+	+	+	-
Pereiopods 1 and 2 +/-										
Biramous +/-	+	R+	+	+	+	+	+	+	+	+
Endopodite - Propodus fixed finger +/-	-	+	+	+	+	+	+	+	+	+
Pereiopod 3 +/-										
Biramous +/-	+	-	R+	R+	+	+	+	+	+	+
Pereiopod 4 +/-										
Biramous +/-	+	-	R+	R+	R+	+	+	+	+	+
Pereiopod 5 +/-										
Biramous +/-	+	-	R+	R+	+	+	+	+	+	+
Abdomen										
Somite 5 - Lateral spines +/-	+	+	+	+	+	+	+	+	+	-
Somite 6 - Continuous with telson +/-	-	+	+	-	-	-	-	-	-	-
Pleopods +/-	+	-	-	-	-	R+	R+	R+	R+	+
Fringing setae	+/ -	+	+	+	+	+	+	+	+	+
Appendix interna 2-5 +/-	+	-	-	-	-	-	-	+	+	+
Telson										
Posterior margin concave (-)/convex (+)	+	+/-	+/-	-	-	+/-	+/-	+	+	+
Spine formula	+4 2+2	7+7	7+7	6+6	4+4	4+4	4+4	4+4	4+4	2+2
Small spines +/-	-	+	+	+	+	+	+	+	+	-
No. of pairs of lateral spines	2	0	0	0	0	0	0	0	0	2
Uropods +/-	32 31	-	-	+	+	+	+	+	+	+
Long plumose setae - Endopodite	32 31	-	-	+	9-11	14-17	17-23	30	34	37
Exopodite	35 37	-	-	10-12	16-19	21-25	23-30	33	35	37

1 N.B. Many of these are estimates from poor-figures in published work; R=rudimentary; +=present/yes; -=absent/no.

